Thesis/
Reports
Whysong,
G. L.

CARBOHYDRATE STUDIES OF SHRUB LIVE OAK AND MOUNTAIN MAHOGANY

Gary Whysong and Kyle Mohan

THESIS
AND
REPORTS
Whysong

FINAL REPORT

CARBOHYDRATE STUDIES OF SHRUB LIVE OAK AND MOUNTAIN MAHOGANY

Submitted by:

Gary Whysong
Assistant Professor and
Principal Investigator

Kyle Mohan
Graduate Research Assistant

16-620-CA

Submitted to:

UNITED STATES FOREST SERVICE

UNITED STATES DEPARTMENT OF AGRICULTURE

December, 1977

LIBRARY COPY
ROCKY MT. FOREST & RANGE
EXPERIMENT STATION

TABLE OF CONTENTS

	PAGE
INTRODUCTION	1
LITERATURE REVIEW	2
STUDY SITE	8
METHODS	11
RESULTS AND DISCUSSION	14
CARBOHYDRATE CYCLES	20
CONCLUSIONS	35
APPENDIX A	36
APPENDIX B	41
LITERATURE CITED	44

LIBRARY COPY
ROCKY MT. FOREST & RANGE
EXPERIMENT STATION

INTRODUCTION

The need for conversion of portions of Arizona chaparral to a different vegetation type to increase water and forage yields and to improve wildlife habitat are increasing. Due to environmental restrictions, the future use of herbicides for conversion is doubtful. Prescribed burning offers promise as an economical and environmentally acceptable alternative. Since most Arizona chaparral species sprout vigorously following fire, there is a need to determine the point at which fire is most apt to be detrimental to regrowth. This point is likely to be at the time when removal of the carbohydrate producing tissues will most limit production and storage.

Research to investigate carbohydrate levels in two chaparral species, funded by cooperative agreement 16-620-CA, was initiated in June, 1976. The objectives of the study were to accomplish the following:

1. Determine carbohydrate cycles of shrub live oak (Quercus turbinella) and mountain mahogany (Cercocarpos betuloides) during the annual growth and dormancy period.

2. Determine the period of maximum carbohydrate depletion of the two shrub species. Generally this period is considered the point when control will be most effective.

3. Determine what relationships exist among carbohydrate cycles, precipitation, soil moisture, air temperature and phenology of the shrubs.

LITERATURE REVIEW

Numerous studies have been conducted to determine the carbohydrate (CHO) trends of perennial plants. It has been found that most herbacous perennials exhibit similar cycles of CHO storage and depletion. Generally, a low point is reached during rapid growth and maximum storage is attained at maturity (McCarty, 1935; McCarty and Price 1942; Troughton, 1957; Mooney and Billings, 1960; Weinmann, 1961; Menke, 1973).

Research conducted on woody species has revealed, in many cases, similar cycling of carbohydrate reserves. Kramer and Kozlowski (1960) found that, in general, deciduous plants achieve maximum CHO accumulation near the time of leaf fall, and experience a decline in stored food during rapid spring growth. Wood et.al. (1959) determined that the roots of the deciduous plants blue jack oak (Quercus incana) and turkey oak (Q. laevis) reached minimum CHO levels at the beginning of May, when new leaves had reached full size. Generally, CHO increased from this low point, and peaked in November at leaf fall. Boo and Pettit (1975) noted a similar pattern in the CHO cycle of sand shin oak roots (Quercus havardii), a rhizomatous, deciduous shrub. Donart (1969) studied CHO reserves of six mountain range plants, including the shrubs little rabbitbrush (Chrysothammus viscidiflorus) and snowberry (Symphoricarpos vaccinioides). Root samples of both species reached a low point in stored CHO in May, during early leaf stage. CHO levels fluctuated, following this low point, but generally increased over summer. Maximum reserves were present by plant maturity. Coyne and Cook (1970) studied eight desert range species, including five shrubs. They observed CHO trends in Shadscale (Atriplex confertifolia), Nuttal saltbush (Atriplex falcata), and winterfat (Eurotia lanata), similar to those described by Donart (1969).

Wright and Stinson (1970) and Wilson et. al. (1975) determined that the low point in the storage cycle of mesquite roots was reached when leaves were nearly full grown, and early spring growth was being completed. Maximum levels were reached in the autumn. Menke (1973) studied CHO trends of roots and crowns of nine Colorado range species and observed a spring depletion and maximum autumn accumulation in the stored CHO of all species except James cryptantha (Cryptantha jamesii).

CHO During Dormancy

During times of dormancy or quiescence, plants continue to draw on CHO reserves (Weinmann, 1961). Generally, winter respiration results in a late winter decline in CHO levels of deciduous plants (Kramer and Kozlowski, 1960). Coyne and Cook (1970) reported an overwinter loss in total available carbohydrates of roots and crowns of big sage, Nuttal saltbush and winter fat. Percent declines in root and crown CHO storage respectively were 50% and 27% for big sage, 20% and 17% for Nuttal saltbush, and 17% and 18% for winter fat.

CHO and Fruit Development

Another factor which causes CHO reduction is fruit development. Large quantities of CHO are needed for seed development (Kramer and Kozlowski, 1960), and fruit development is apparently responsible for mid-summer CHO declines (Jameson, 1963). Coyne and Cook (1970) found that big sage began its decline in stored CHO about the time of early seed stage. McConnell and Garrison (1966) and Menke (1973) agreed that the low point of root and crown CHO of bitterbrush (Purshia tridentata) occurred during fruiting.

CHO in Plant Parts

Cook (1966) reported that CHO can be stored in all plants parts. However, TAC (total available carbohydrates) are generally greater in root material than top material (McConnell and Garrison, 1966). Those organs containing the most

TAC, exhibit the greatest seasonal fluctuations (McConnell and Garrison, 1966; Coyne and Cook, 1970; Menke, 1973). McConnell and Garrison (1966) sampled large and small roots, current twigs, one year old twigs and over one year old twigs of bitterbrush. They found that small roots (less than .25 inch) had the highest percent concentration of CHO, the greatest total weight of CHO, and exhibited the most pronounced seasonal fluctuations.

CHO in Evergreen Plants

Generally, evergreen plants exhibit different CHO cycling trends than deciduous species. Usually, there is much less fluctuation in CHO levels of evergreen species than in deciduous species, because evergreens seem to be more dependent on current photosynthesis than storaged CHO for shoot growth in spring (Kramer and Kozlowski, 1960; Mooney et. al. 1973). Evergreen plants tend to accumulate, rather than deplete, carbohydrate reserves overwinter (Kramer and Kozlowski, 1960). Mooney et. al. (1973) reports that evergreen shrubs of the chaparral type are able to carry out photosynthesis yearlong, during most years, but at reduced rates during summer drought. Coyne and Cook (1970) theorized that a slight increase in TAC levels of roots and twigs of big sage during spring growth occurred because existing leaves were more than sufficient to provide CHO during the initial spring flush of growth. However, stored CHO in big sage declined overwinter. Hepting (1945) and Sablon (1906) studied CHO content of roots and stems of Pinus echinata and Pinus australis, respectively, and reported similar findings. Both workers found that reserves were lowest in the autumn, but increased overwinter to a maximum level in early spring. Cormack and Bate (1976) reported that the wood, bark and leaves of the perennial evergreen tree, Macadamia integrifolia accumulated CHO both in midsummer and winter. The first period of accumulation was followed by a rapid depletion corresponding to a spring flush of growth and the winter accumulation was followed by a secondary growth period including fruit-set in late summer-early autumn.

Mooney and Hays (1973) reported relatively minor fluctuations in CHO both in leafy-stems of the evergreen, coastal live oak. However, the TAC values were higher overwinter than during spring growth and fruiting.

Seasonal Variability in CHO Trends Growth Behavior and Abiotic Factors

Seasonal variability in TAC is primarily attributed to growth behavior and variable environmental conditions (Cook 1966). Coyne and Cook (1970) maintain that stage of plant growth is the single most important factor influencing TAC reserves. Wilson et. al. (1975) found large differences in TAC levels in mesquite trees of varying reproductive potential. Menke (1973) reported that minimum TAC values of fourwing saltbush occurred during twig elongation in two successive years, although the time of twig elongation varied by two weeks.

Abiotic factors affecting growth have been cited as explanation for yearly variations in seasonal CHO storage trends. Rising temperature, apparently, greatly increases the use of stored food in respiration (Kramer and Kozlowski, 1960). Laude et. al. (1961) discovered that the appearance of new growth in chamise varied by as much as two months, depending on environmental conditions. Twig growth began within the narrow daytime temperature range of 12 to 16 degrees C and night time range of 3 to 6 degrees C. Watkins and DeForest (1941) reported that elongation of chamise stems ceased when air temperatures reached a minimum of 7 degrees C. Photosynthesis exceeded respiration in conifers, when air temperatures were above -6 degrees C (Freeland, 1944). Air temperature appeared to affect inversely CHO storage in orchardgrass during spring growth. Low temperatures resulted in CHO accumulation and high temperatures in depletion (Colby et. al., 1966). Feltner and Massengale (1965) reported more variability in TAC levels of alfalfa roots with maximum temperatures, than with other measurements of temperature. High soil temperatures caused losses of sucrose and fructosan from rye grass roots, which resulted in exhaustion and, in some cases, death of roots (Sullivan and Sprague, 1949).

The amount and distribution of precipitation, through its affect on growth, likewise, induced variability in seasonal TAC cycles (Menke, 1973). Lack of sufficient moisture, early in the growing season, resulted in lower levels of CHO stored in the autumn in big sage and black sage in a two year study by Trlica and Cook (1971). Autumn rains caused renewed growth activity in black sage, and resulted in an earlier fall decline in TAC than previously recorded (Coyne and Cook, 1970).

Moisture stress apparently decreases CHO use in cotton (Eaton and Ergle, 1948), and generally, moisture stress is associated with increased CHO reserves (Eaton and Erlge, 1948; Brown and Blaser, 1965; Blaser, Brown and Bryant, 1966; Brown and Blaser, 1970; Maranville and Paulsen, 1970; Sosebee and Wiebe, 1971; Trlica, 1971; Dina and Klikoff, 1973). An early frost was blamed for a drop from 18.5% to 6% starch in samples of grape vines, collected on Nov. 1 and Nov. 6 respectively, in two successive years (Winkler and Williams, 1945).

Absence of CHO Trends and Unexplained Fluctuations

Absence of distinct seasonal CHO trends and unexplained fluctuations have been reported by several researchers. Mooney and Hays (1973) reported very little change in CHO content of leafy stems of coastal live oak. Wenger (1953) found no significant change in stem CHO in sweetgum (Liquidambar styraciflua). Coyne and Cook (1970) found no real seasonal trends in TAC of big sage crowns, nor any clearly pronounced trends in the root CHO of this species. TAC levels in crowns of black sage fluctuated erratically throughout the growing season (Coyne and Cook, 1970). Donart (1969) also observed unexplained fluctuations in root reserves of snowberry and little rabbitbrush throughout the period of build up. Hepting (1945) sampled roots and stems of short leaf pine at two different locations and reported an unexplained dip in the reserve CHO of root bark in June at one location, without a corresponding reduction at the second

location. Boo and Pettit (1975) observed an increase in CHO of sand shin oak roots, before the plant broke dormancy. Menke (1973) found an overwinter increase in the TAC of fourwing saltbrush stems and a decrease during bud swell in 1971. These trends were reversed in 1972. Cormack and Bate (1976) found that the CHO of individual macadamia shoots exhibited somewhat irregular trends. Smith et. al. (1952), and Cameron et. al. (1952), working with citrus, also observed erratic fluctuations within the overall CHO storage cycle.

STUDY SITE

The study site was established on the Sierra Ancha Experimental Forest, T.5N., R.13E., sec 11, NE ¼ NE ¼. The area was characterized by a north-south ridge with east and west exposure slopes at an elevation of about 1680 meters. Vegetation consisted of largely woody chaparral species dominated by shrub live oak and mountain mahogany, characteristic of the Quercus turbinella - Cercocapus betuloides community type (Carmichael, 1976). The east exposure study area had a 29% slope, while the study site on the west exposure is characterized by a 19% slope.

Both exposures were densely covered by chaparral plants. The total canopy cover on the east exposure was 93%, and the total canopy cover on the west exposure was 92%. However, differences in species composition were evident. The most notable difference, was the presence of Pinus ponderosa and Quercus arizonica on the west exposure, indicative of a more mesic microclimate (Table 1).

Precipitation data collected during this study revealed that the west exposure was,in fact, slightly more mesic. The average monthly precipitation on the west exposure was 3.65 cm, while average monthly precipitaiton on the east exposure was only 3.41 cm.(Appendix A). In addition, there was more soil moisture present at -4 and -80 cm. depths on the west exposure than on the east exposure, at nearly every sampling date (Appendix B).

Air temperature data indicated that the west exposure had more mild temperature fluctuations throughout the year. A comparison of average air temperatures on the two exposures showed that the east exposure was generally hotter than the west exposure during the summer, and the west exposure was warmer than the east exposure during the winter (Appendix A). Also, the minimum temperatures were generally higher on the west exposure. Thus, precipitation, soil moisture and air temperature data indicate that the west exposure had a slightly more

Table 1. Mean canopy cover (%) of plant species occurring on east and west exposure study areas.

SPECIES	Slope Exposure EAST	WEST
Agave Parryi	.0	0.2
Arctostaphylos pringli	1.4	2.9
Arctostaphylos pungens	13.0	26.3
Ceanothus Greggii	3.0	.3
Cercocarpus betuloides	17.7	23.0
Eragrostis curvula	T[1]	.0
Eriodictyon angustifolium	5.0	.0
Nolina microcarpa	1.2	.0
Pinus ponderosa	.0	T[1]
Quercus arizonica	.0	.2
Quercus turbinella	43.9	31.2
Yucca baccata	7.8	7.9

[1]T = trace

mesic microclimate, and experienced more moderate temperatures, typical of a more mesic microclimate. The contrast in species composition of these two exposures apparently results from these differences in microclimate.

METHODS

Tissue samples of the two Arizona chaparral species Cecocarpus betuloides and Quercus turbinella were collected at three week intervals* on the east and west exposures of a north-south ridge at an elevation of about 1680 meters. Sampling commenced on July 10, 1976 and was concluded on July 23, 1977. Tissue samples of three plants of each species on each exposure were collected. Plants to be sampled were chosen in pairs, each pair consisting of one plant of each species. Three plant pairs were selected on each exposure at fifteen pace intervals perpendicular to the ridge line. Care was taken to select only healthy mature plants. Three plant parts, large roots, small roots, and stems were clipped from each plant. Large roots were greater than ¼ inch in diameter, small roots were less than ¼ inch, and all stems selected were greater than ¼ inch. Plants were excavated to a depth of about 50 centimeters. Roots with dead spots or an unhealthy appearance were not collected. All plant tissue was sealed in airtight plastic bags after clipping. After sampling was completed, plant tissue was soaked in 95% ethonol to retard further biological breakdown of CHO (Donart, 1969), and again sealed tightly in plastic bags. Prior to oven drying, plant samples were cleaned with water to remove soil and debris, placed in paper bags, and dried in a force draft oven. Samples were dried at 70°C for 72 hours, and then ground in a Wiley mill to pass through a 40-mesh screen. Ground tissue was stored in air-tight glass vials until the time of chemical analysis. Prior to chemical analysis, all ground material was dried to a constant weight.

*except 4-23-77

Chemical Analysis

Chemical analysis to determine total available carbohydrate (TAC) was performed according to the method described by Smith et. al. 1964. Approximately one half gram of plant material (weight recorded to the fourth decimal place) was placed in a 200 ml round bottom boiling flask. Fifty milliliters of .2N H_2SO_4 were added to the ground material. Flasks were then randomly placed in a hot ethylene glycol bath at 100° for one hour, and agitated at twenty minute intervals. Extract was filtered through a Buchner tunnel, neutralized, and diluted to a volume of 250 ml.

TAC concentration was determined on a glucose equivalent basis according to the Shatter-Somogyi iodometric method as described by Heinze and Murneck (1940) with the modification of reagents set forth in the Association of Official Agricultural Chemists (A.O.A.C), 1965. Ten milliliters of extract were removed from the 250 milliliter volumetric flask and piped into a 250 ml Erlymyer flask. Ten milliters of reagent "50" (A.O.A.C., 1965) were added to the extract. The solutions were then stirred, covered with a funnel, and randomly placed in a hot bath (100°C) for fifteen minutes. Samples were removed and cooled for three minutes in a running cold water bath. Two milliliters of KI-$K_2C_2O_4$ solution were added, then ten milliliters of 1.ON H_2SO_4 were added to the solution, while stirring. Samples were then placed in a cold water bath for fifteen minutes with occasional stirring. Sample solutions were then titrated with a 0.02N sodium thiosulfate solution, using starch as an indicator. Values, measured in milliliters of titrate, were subtracted from a blank reading and multiplied by a reagent standardization factor and by a dilution factor to obtain percent total available carbohydrate of dry matter. Sugar solutions were run prior to the initiation of chemical analysis and at various times throughout analysis, to confirm the accuracy of the procedure. Duplicate

samples were run periodically to check procedure and standard solutions, or whenever a particular determination was unusual or in doubt for any reason (Menke, 1973).

Environmental Measurements

All sampling procedures were conducted jointly on adjacent east and west exposure slopes in the study area. Rain gauges, instrument shelters, hygrothermographs, maximum-minimum thermometers, and gypsum soil moisture resistance blocks were established on each of the two exposures. With the exception of hygrothermograph charts, which were collected weekly, precipitation, soil moisture, maximum and minimum temperature data were collected at each sampling period.

Rain guages consisted of plastic cylindrical cans located on steel posts approximately 1.2 m above the ground surface on each study area. Maximum-minimum thermoters were used in addition to hygrothermographs, because of occasional malfunctions.

Gypsum soil moisture resistance blocks were established at one location on each of the two study areas. Moisture blocks were placed at -5, -20, -40, and -80 cm below the ground surface. Soil samples were collected at each location and depth for calibration of the resistance blocks.

Phenology

The phenology of each species was charted throughout the study. There seemed to be no difference in the phenological stage of each species due to exposure. Thus, for each observation date, there was only one phenological stage listed for each species. The phenological stage recorded represents the stage of development of the majority of the plants of one species at each observation date.

RESULTS AND DISCUSSION

Environmental Factors, Phenology and Total Available Carbohydrates

In an attempt to describe the relationship between environmental factors, phenology, and carbohydrate levels of the plant parts of Cercocaupus betuloides and Quercus turbinella, backward stepwise regression analysis was performed using all data collected during this yearlong study. The models were constructed in such a way that the standard error was reduced to a minimum while maintaining significance at the .05 probability level (except as noted). Unfortunately, these models did not yield an acceptable description of the ecological interactions under examination, and may be used for predictive purposes only. Although the standard error was minimal, these models, on the average, could account for only 50% of the variation of the response variable. Thus, their predictive ability was limited as well.

The following phenological stages were included as variables in the regression analysis of Cercoacarpus betuloides CHO levels: new leaf formation, rapid vegetative growth, reduced growth, mature flower, seed formation, seed fill, mature seed, seed fall, and winter rest. The phenological stages of Quercus turbinella included in the analysis were: bud swell, new leaf formation, flower, mature flower, seed formation, seed fill, mature seed, seed fall, reduced growth, and winter rest. The environmental factors included as independent variables for both species were: exposure, average air temperature, soil moisture at depths of 5, 20, 40, and 80 centimeters and precipitation. Each of the six models is discussed below.

Cercocarpus betuloides - Large Roots

The regression model, with CHO content of large mountain mahogany roots as a response variable, had a multiple correlation coefficient of .74, a standard error of the response variable of 11.17 mg/g and explained 54.5% of the variation

of the dependent variable. The model and variables were as follows:

$$\hat{Y} = 140.38 - 25.20X_1 + 16.08X_2 + 17.70X_3 + 31.80X_4 - .98X_5 + 1.46X_6$$

Where:

X_1 = new leaf formation

X_2 = reduced growth

X_3 = flower maturity

X_4 = seed formation

X_5 = minimum air temperature (°F)

X_6 = precipitation

The variable minimum air temperature had the greatest standard partial regression coefficient, and thus was the most important variable in the model. In addition, minimum air temperature was the only variable significantly ($P = .05$) correlated ($r = .37$) with CHO levels of mountain mahogany large roots.

Cercocarpus betuloides - Small Roots

This model explained only 32% of the variation in the CHO levels of mountain mahogany small roots. The multiple correlation coefficient was .56. The standare error of the response variable was 13.29 mg/g. The model and variables were as follows:

$$\hat{Y} = 145.75 + 17.39X_1 - 56X_2$$

Where:

X_1 = reduced growth

X_2 = minimum air temperature (°F)

The variable with the greatest standard partial regression coefficient was minimum air temperature. The only two variables to exhibit a significant (P = .05) level of correlation with the response variable were minimum air temperature, and the phenological stage winter rest (r = .42, and .38, respectively).

Cercocarpus betuloides - Stems

The multiple correlation coefficient of this model was .68. The standard error of the response variable was 8.14 mg/g; 46% of the variation in CHO content of mountain mahogany stems was explained. The model and variables were as follows:

$$\hat{Y} = 89.65 + 14.04X_1 + 24.51X_2 - .55X_3$$

Where:

X_1 = mature flower

X_2 = seed formation

X_3 = minimum air temperature (°F)

The variable, minimum air temperature, had the largest standard partial regression coefficient. The variables minimum air temperature and mature seed were the only independent variables with a significant (P = .05) degree of association with the response variable (r = .45, and .33, respectively).

Quercus turbinella - Large Roots

This model explains 77.8% of the variation in the CHO levels of shrub live oak large roots. The multiple correlation coefficient was .88. The standard error of the response variable was 9.15 mg/g. The model and variables were as follows:

$$\hat{Y} = 172.64 - 15.69X_1 + 28.88X_2 + 74.34X_3 + 54.69X_4 + 18.50X_5 + 36.64X_6 - .91X_7 - .70X_8 - .72X_9 + .49X_{10}$$

Where:

X_1 = new leaf formation

X_2 = seed formation

X_3 = seed fill

X_4 = mature seed

X_5 = seed fall

X_6 = reduced growth

X_7 = maximum air temperature (°F)

X_8 = minimum air temperature (°F)

X_9 = soil moisture, -40 cm

X_{10} = soil moisture, -80 cm

The standard partial regression coefficients revealed that the three most important variables in the model were maximum air temperature, and the phenological stages, seed fill and seed maturity. However, the only independent variables that were significantly (P = .05) associated with the response variable were seed fill and new leaf formation (r = .31, and .35, respectively).

Quercus turbinella - Small Roots

Only 37.8% of the variation in CHO content of shrub live oak small roots was explained by this model. The model had a multiple correlation coefficient of .62. The standard error of the response variable was 10.04 mg/g. The model and variables were as follows:

$$\hat{Y} = 144.24 + 26.79X_1 + 15.42X_2 + 14.24X_3 - .55X_4 + .39X_5$$

Where:

X_1 = seed fill

X_2 = mature seed

X_3 = reduced growth[1]

X_4 = maximum temperature (°F)

X_5 = soil moisture, -5 cm

The variables maximum air temperature and seed fill had the highest standard partial regression coeficients. The only independent variable significantly (P = .05) correlated with the response variable was soil moisture at-5 cm (r = .33).

Quercus turbinella - Stems

This model had a multiple correlation coefficient of .73, a standard error of the response variable of 7.94 mg/g, and explained 54% of the variation in the CHO content of shrub live oak stems. The model and variables were as follows:

$$\hat{Y} = 93.71 + 34.94X_1 + 25.20X_2 + 20.37X_3 - .85X_4 - .42X_5$$

Where:

X_1 = seed fill

X_2 = mature seed

X_3 = reduced growth

X_4 = minimum air temperature (°F)

X_5 = soil moisture, -40 cm

[1]Statistically significant at the .1 probability level.

No independent variable was significantly (P = .05) correlated with stem CHO levels. The variable with the largest standard partial regression coefficient was the minimum air temperature.

Environmental Factions - Phenology and TAC Summary

In each of the three regression models predicting CHO levels of Cercocarpus, the variable minimum air temperature was negatively related with CHO levels of the three plant parts. Also, this variable had the largest standard partial regression coefficient in the models with Cercocarpus large roots and stems as response variables. Although the variable winter rest was not included in the regression model with Cercocarpus small roots as the response variable, winter rest did show a significant positive correlation with CHO levels of small roots. Thus, a general association was indicated between lower air temperatures and higher CHO levels of mountain mahogany plant parts. This conclusion is consistant with the observation made by Kramer and Kozlowski (1960), that evergreen plants tend to accumulate stored carbohydrates during winter months, due to reduced respiration and cessation of tissue elongation.

The phenological stage seed fill had the highest standard partial regression coefficient, and thus, was the most important variable in two of the three models predicting CHO levels in the plant parts of Quercus turbinella. There was a positive association (P = .05) between this variable and CHO levels of shrub live oak large roots. However, there was no significant (P = .05) association between seed fill and CHO levels of small roots and stems of shrub live oak.

The failure of these models to accurately predict CHO levels was probably due to the lack of distinct trends present in the CHO cycles of these plants. This subject is discussed more thoroughly in the latter sections of this paper.

CARBOHYDRATE CYCLES

A four factor factorial analysis of variance was performed on all carbohydrate data collected during the study. The experimental design was a randomized complete block with position on slope constituting blocks. The four factors were: 1 exposure, 2 species, 3 plant part, and 4 time. Factor one, exposure, consisted of two levels, east and west, while the two plant species were the two levels of factor 2. Factor three, plant parts, consisted of large roots, small roots and stems while factor four, time, represented 20 levels of observation dates when field sampling was conducted. All tests of significance were conducted at the .05 probability level and highly significant differences (P = .01) were noted.

Results indicated that neither position on slope or exposure significantly affected CHO levels of the shrub species during the study period. Carbohydrate levels in mountain mahogany were significantly higher than in turbinella oak on both slope exposures. A highly significant difference was found with respect to plant parts of the two shrub species. Comparison of plant parts revealed that CHO levels of large roots, small roots and stems of mahogany, in each case, were significantly greater than TAC levels of the corresponding plant parts of oak.

Since slope exposure was non-significant, data were subsequently analyzed as four discrete two factor factorial problems. Species and exposure were eliminated as factors. This resulted in plant parts and time as the two factors investigated for each individual species. Such a procedure facilitated interpretions of results associated with numerous significant differences occurring over the 20 sampling periods.

Cercocarpus betuloides - East Exposure

On the east exposure, average TAC levels of small mountain mahogany roots were significantly greater than average TAC levels of stem tissue at every sampling period except 8-21-76 (Figure 1). On 8-21-76, during the phenological stage seed formation, a decline in CHO content of mahogany small roots coincided with an increase in CHO content of stem tissue, and resulted in CHO levels not significantly different at the .05 probability level. In addition, there was no difference between CHO levels of large roots and levels of stems on this date. Average CHO levels of mountain mahogany large roots were significantly greater than stem values on eight of the twenty sampling dates. The only significant difference between average TAC levels of mahogany large and small roots occurred on 12-26-76, during the phenological stage of winter rest.

Two major peaks occurred in the CHO cycle of both large and small roots of mountain mahogany on the east exposure. The first peak occurred on 1-15-77, during the period of winter rest 11-13-76 to 3-19-77. The TAC level of mahogany roots collected on 1-15-77 was significantly greater than the CHO level of roots in the preceeding phenological stage, seed fall, and in the following stage, new leaf formation (Table 2). A second peak period of CHO accumulation was found in root tissue collected on 6-11-77. It was at about this time, that the phenology changed from a stage of rapid vegetative growth, to a stage of much reduced growth, due to summer drought. Plants were still in this latter phenological stage at the conclusion of sampling on 7-23-77. However, TAC levels measured in root samples collected on 6-11-77 were significantly greater than levels from the 7-23-77 sampling period. Mooney, Parsons and Kummerow (1973) state that evergreen shrubs of the mediterranean type climates generally photosynthesize at reduced levels during summer drought. Possibly, this summer drought contributed to the decline in CHO levels of mountain mahogany roots on this exposure.

Figure 1. Plant phenology and total available carbohydrates of selected plant parts of mountain mahogany on the east exposure study area. (July 1976-July 1977)

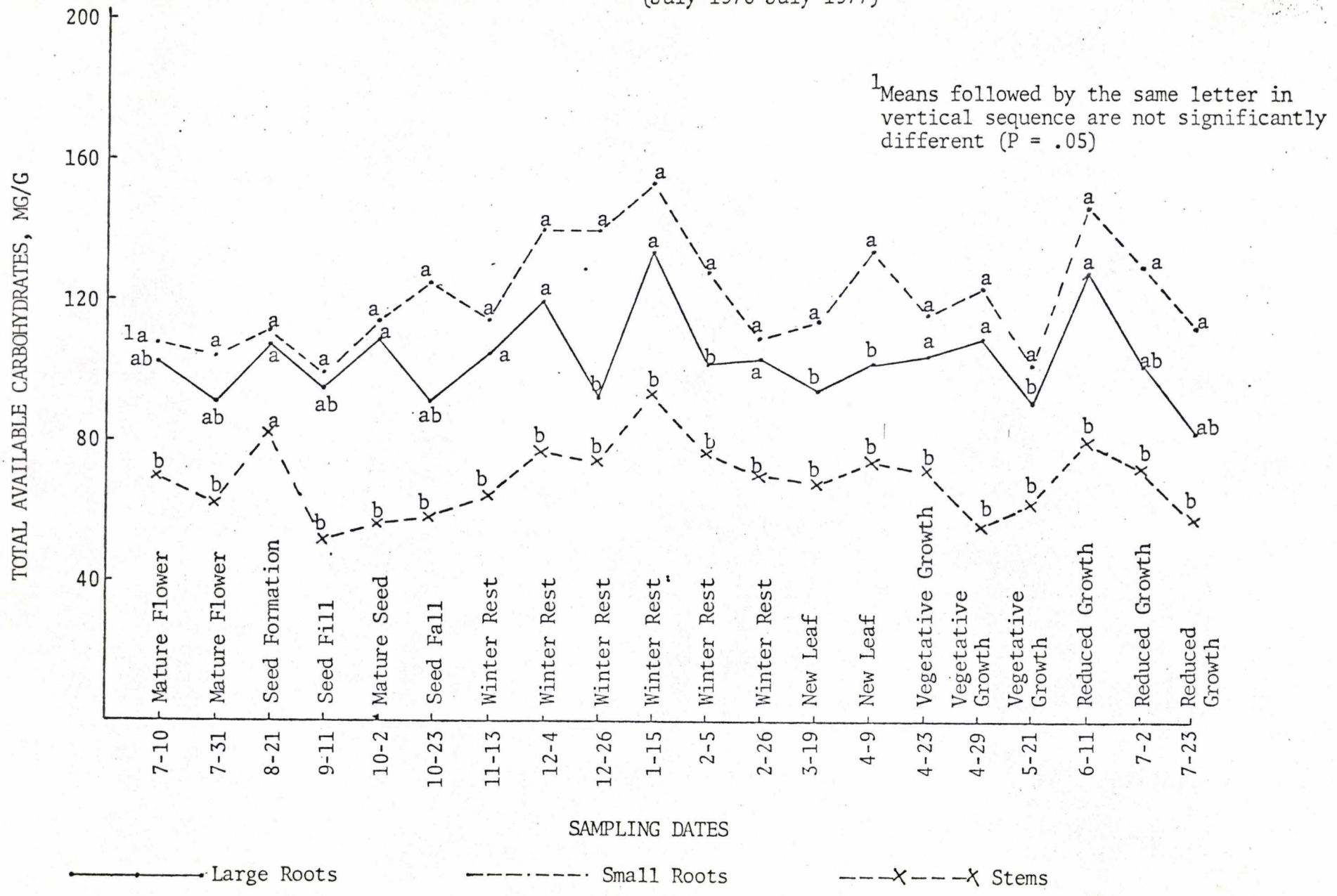


Table 2. Mean carbohydrate content (mg/g) of large roots, small roots and stems of mountain mahogany on the east exposure study area.[1] (July 1976-July 1977)

Sample Date		Large Roots	Small Roots	Stems
1.	7-10-76	103.2 abcd	108.2 cde	70.4 ab
2.	7-31-76	91.2 cd	105.2 cde	62.1 ab
3.	8-21-76	107.3 abcd	110.0 cde	83.0 ab
4.	9-11-76	96.3 bcd	100.0 e	51.5 b
5.	10-2-76	109.5 abcd	113.5 cde	56.6 b
6.	10-23-76	91.5 cd	124.9 abcde	59.2 b
7.	11-13-76	106.0 abcd	115.2 cde	65.1 ab
8.	12-4-76	120.0 abc	139.9 abcd	78.1 ab
9.	12-26-76	93.2 bcd	139.7 abcd	75.0 ab
10.	1-15-77	134.7 a	154.2 a	94.6 a
11.	2-5-77	103.4 abcd	129.0 abcde	77.1 ab
12.	2-26-77	105.0 abcd	109.8 cde	69.6 ab
13.	3-19-77	96.3 bcd	115.2 cde	68.1 ab
14.	4-9-77	104.4 abcd	134.1 abcde	74.5 ab
15.	4-23-77	106.7 abcd	116.8 bcde	71.1 ab
16.	4-29-77	109.9 abcd	124.1 abcde	55.5 b
17.	5-21-77	91.4 cd	103.2 e	61.8 ab
18.	6-11-77	129.2 ab	147.6 ab	80.1 ab
19.	7-2-77	103.9 abcd	130.1 abcde	71.9 ab
20.	7-23-77	82.6 d	113.8 cde	58.8 b

[1]Means followed by the same letter in vertical sequence are not significantly different (P = .05)

Carbohydrate levels in mountain mahogany stems on the east exposure also significantly increased during the middle of the winter rest period. The average CHO level in stem tissue collected on 1-15-77 was significantly greater than the levels attained during the phenological stages of seed fill, seed maturity, and seed fall. This CHO level was also greater than the level of CHO present in stem tissue on 7-23-77, when mountain mahogany plants were in a state of much reduced growth.

Cercocarpus betuloides - West Exposure

TAC trends of Cercoacarpus betuloides on the west exposure were somewhat similar to those found on the east exposure (Figure 2). On the west exposure, average small root levels were significantly greater than stem levels in seventeen of the twenty sampling periods examined. No differences were observed on dates 7-10-76, 8-21-76 and 3-19-77, during the phenological stages mature flower, seed formation and new leaf formation respectively. On each of these dates, CHO levels of stems showed an upward trend, while small roots showed a downward trend. Average large root TAC levels were significantly greater than stem levels on nine of the twenty sampling dates, including 8-21-76. Average small root TAC levels were significantly greater than average large root levels on 4-9-77, during the phenological stage new leaf formation.

Large roots and small roots of Cercocupus on the west exposure, as on the east exposure, attained a maximum level in the CHO storage cycle on 1-15-77, during the period of winter rest. CHO concentrations present in tissue sampled on this date marked the only dramatic peak in the CHO trends of small mahogany roots on this exposure (Table 3). The TAC level of small roots on 1-15-77 significantly exceeded the level present at sixteen of the nineteen other sampling dates, including levels found during seed fall, new leaf formation the preceeding and following phenological stages, respectively. CHO concentration in large roots, however, remained at

Figure 2. Plant phenology and total available carbohydrates of selected plant parts of mountain mahogany on the west exposure study area. (July 1976-July 1977)

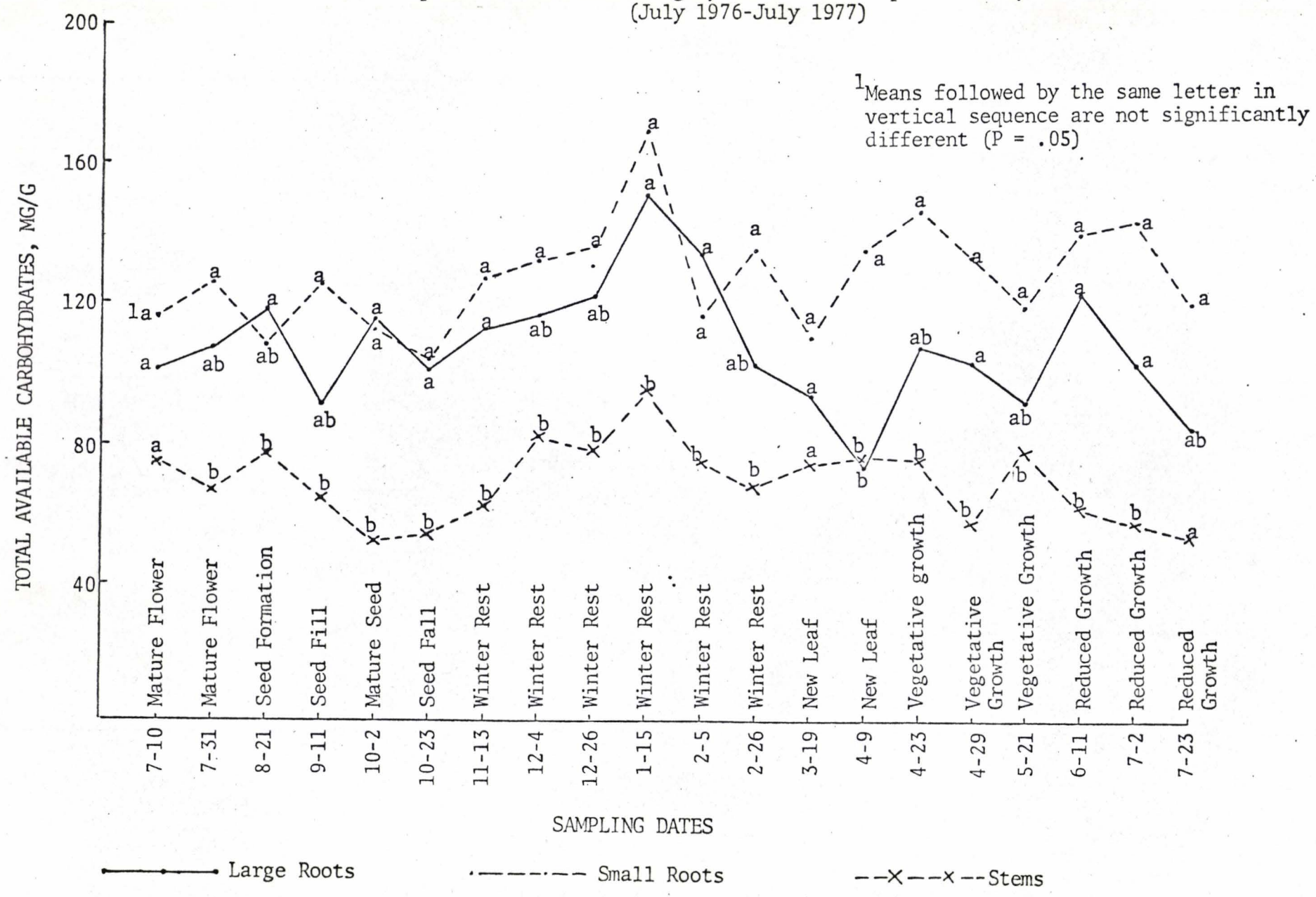


Table 3. Mean carbohydrate content (mg/g) of roots, small roots and stems of mountain mahogany on the west exposure study area.[1] (July 1976-July 1977)

Sample Date	Large Roots	Small Roots	Stems
1. 7-10-76	102.0 bcdef	116.0 bc	74.7 ab
2. 7-31-76	108.5 bcdef	125.6 bac	67.4 ab
3. 8-21-76	119.4 bcdef	108.7 bc	77.7 ab
4. 9-11-76	91.4 cdef	126.5 bc	65.5 ab
5. 10-2-76	115.8 abcdef	112.1 bc	51.8 b
6. 10-23-76	101.3 bcdef	104.2 c	55.2 ab
7. 11-13-76	112.5 abcdef	128.2 bc	63.2 ab
8. 12-4-76	116.5 abcdef	132.9 bc	81.5 ab
9. 12-26-76	123.0 abcd	136.8 bc	78.7 ab
10. 1-15-77	150.9 a	169.8 a	95.5 a
11. 2-5-77	134.7 ab	117.1 bc	74.9 ab
12. 2-26-77	103.0 bcdef	136.1 bc	69.3 ab
13. 3-19-77	94.4 bcdef	109.8 bc	74.7 ab
14. 4-9-77	74.2 f	135.6 bc	75.3 ab
15. 4-23-77	108.3 bcdef	148.0 ab	76.5 ab
16. 4-29-77	103.3 bcdef	133.3 bc	59.4 ab
17. 5-21-77	91.9 cdef	120.5 bc	79.4 ab
18. 6-11-77	124.1 abc	139.8 abc	63.5 ab
19. 7-2-77	102.4 bcdef	144.3 abc	59.4 ab
20. 7-23-77	86.3 cdef	121.1 bc	54.3 b

[1]Means followed by the same letter in vertical sequence are not significantly different (P = .05)

a high level from 1-15-77 until 2-26-77, the advent of new leaf formation. There were no major increases in TAC levels of mountain mahogany stem tissue on this exposure during the entire period in which material was collected.

Thus, root tissue of Cercocarpus betuloides, on both exposures, contained greatest concentrations of total available carbohydrates during the phenological stage of winter rest. However, Cercocarpus root tissue from the west exposure did not exhibit a second peak period of CHO accumulation and subsequent decline during the stage of reduced growth, as was evident on the east exposure.

Quercus turbinella - East Exposure

TAC levels of small roots of shrub live oak were significantly greater than stem levels at every sampling period (Figure 3). CHO levels of oak large roots were significantly greater than stem levels on seven of the twenty sampling dates. Small root TAC levels exceeded large root levels on four sampling dates, 7-31-76, 10-23-76, 4-23-77 and 4-29-77.

TAC levels of Quercus turbinella large roots on the east exposure fluctuated erratically, exhibiting six major periods of CHO accumulation (Table 4). Three of the peaks occurred during winter rest, two during the mature seed stage, and one during seed fill. The CHO cycled of oak small roots and stems showed only one major period of accumulation. This occurred on sampling date 1-15-77, during winter rest.

Quercus turbinella - West Exposure

CHO levels of shrub live oak root tissue on the west exposure exhibited small fluctuations, but did not increase significantly during winter rest, as did all other root tissue previously discussed (Figure 4). However, there was a significant increase in CHO levels of Quercus large roots on 8-21-77, during the mature seed stage (Table 5). TAC levels of small oak roots did increase significantly on 1-15-77, during winter rest. Shrub live oak stems showed no significant differences in TAC levels throughout the yearly CHO cycle.

Figure 3. Plant phenology and total available carbohydrates of selected plant parts of shrub live oak on the east exposure study area. (July 1976-July 1977)

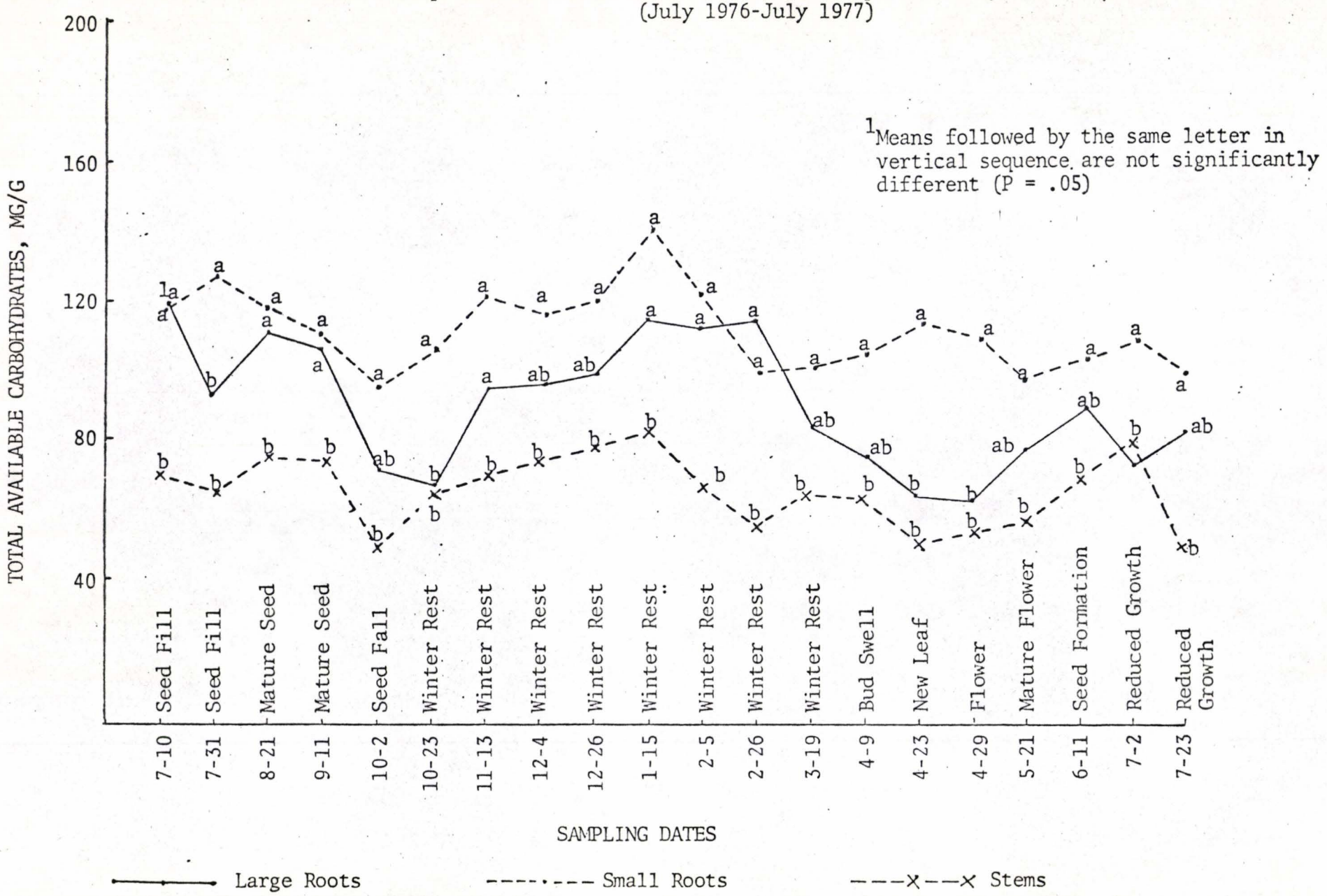


Table 4. Mean carbohydrate content of large roots, small roots and stems of shrub live oak on the east exposure study area.[1] (July 1976-July 1977)

Sample Date	Large Roots	Small Roots	Stems
1. 7-10-76	119.2 a	118.2 ab	70.5 ab
2. 7-31-76	92.9 abcdefghi	127.3 ab	64.2 ab
3. 8-21-76	111.9 abcde	118.5 ab	75.6 ab
4. 9-11-76	106.5 abcdef	109.0 b	73.2
5. 10-2-76	71.4 ghi	95.5 b	49.4 b
6. 10-23-76	67.4 ghi	107.4 b	63.4 ab
7. 11-13-76	96.3 abcdefgh	121.5 ab	70.1 ab
8. 12-4-76	96.7 abcdefg	118.5 ab	71.8 ab
9. 12-26-76	92.9 abcdefghi	119.8 ab	78.0 a
10. 1-15-77	115.8 ab	140.7 a	82.3 ab
11. 2-5-77	113.9 abcd	122.3 ab	64.2 ab
12. 2-26-77	115.8 abc	98.3 b	55.0 ab
13. 3-19-77	85.1 bcdefghi	100.0 b	63.1 ab
14. 4-9-77	74.7 ghi	105.3 b	61.8 ab
15. 4-23-77	65.0 hi	114.3 ab	50.1 b
16. 4-29-77	63.5 i	110.4 b	52.4 ab
17. 5-21-77	76.7 fghi	96.9 b	53.5 ab
18. 5-11-77	90.1 abcdefghi	105.4 b	68.9 ab
19. 7-2-77	73.4 abcdefghi	116.4 ab	79.9 ab
20. 7-23-77	80.4 fghi	99.5 b	49.5 b

[1]Means followed by the same letter in vertical sequence are not significantly different (P = .05)

Figure 4. Plant phenology and total available carbohydrates of selected plant parts of shrub live oak on the west exposure study area. (July 1976-July 1977)

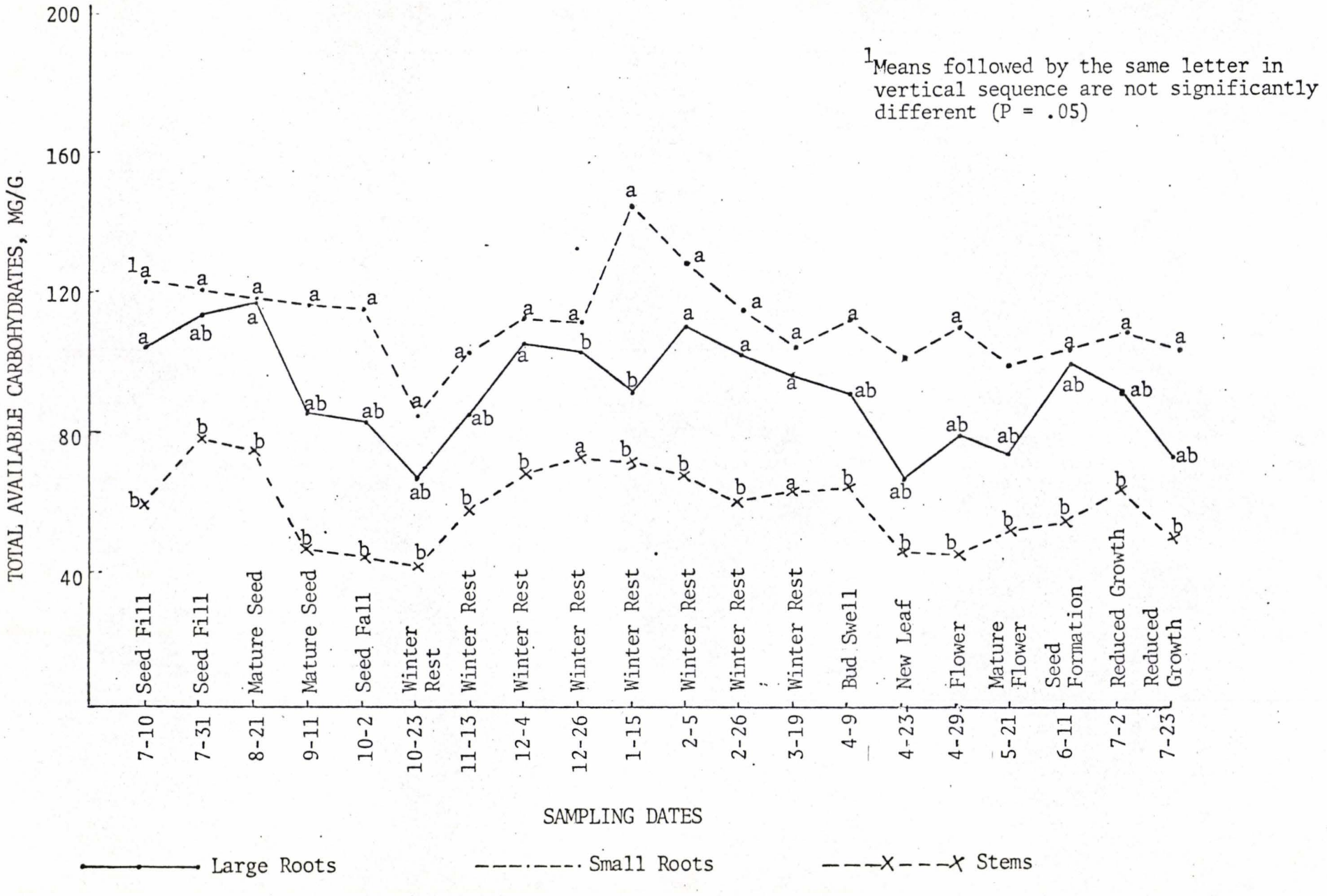


Table 5. Mean carbohydrate content (mg/g) of large roots, small roots and stems of shrub live oak on the west exposure study area. [1] (July 1976-July 1977)

Sample Date	Large Roots	Small Roots	Stems
1. 7-10-76	102.6 abcde	121.6 abc	60.4 a
2. 7-31-76	113.0 abc	120.2 abc	77.7 a
3. 8-21-76	117.3 a	118.1 abc	74.2 a
4. 9-11-76	85.7 abcde	115.5 abc	47.2 a
5. 10-2-76	81.9 abcde	114.6 abc	44.6 a
6. 10-23-76	68.2 e	84.3 c	41.4 a
7. 11-13-76	86.5 abcde	102.4 bc	59.0 a
8. 12-4-76	114.4 ab	113.2 abc	69.3 a
9. 12-26-76	102.2 abcde	110.6 abc	71.7 a
10. 1-15-77	90.4 abcde	144.1 a	71.0 a
11. 2-5-77	110.5 abcd	128.7 ab	69.4 a
12. 2-26-77	101.4 abcde	116.5 abc	60.6 a
13. 3-19-77	96.8 abcde	103.1 bc	62.9 a
14. 4-9-77	92.4 abcde	114.3 abc	64.8 a
15. 4-23-77	67.7 e	99.6 bc	47.1 a
16. 4-29-77	79.8 abcde	109.3 abc	46.0 a
17. 5-21-77	75.2 bcde	98.1 bc	53.6 a
18. 6-11-77	98.3 abcde	104.7 bc	58.6 a
19. 7-2-77	91.3 abcde	110.5 abc	66.3 a
20. 7-23-77	75.6 bcde	106.2 abc	49.2 a

[1] Means followed by the same letter in vertical sequence are not significantly different (P = .05)

Carbohydrate Trends - Summary

The comparison of the TAC levels of plant parts of each species on each slope revealed that, generally, the root tissue contained a greater amount of CHO than stem tissue. In nearly every observation, TAC levels of small root tissue of a species exceeded levels of stem tissue of the same species. TAC levels of large shrub live oak roots exceeded stem levels on approximately 30% of the sampling dates. TAC levels of mountain mahogany large roots were significantly greater than mahogany stems on approximately 42% of the sampling dates. The large and small roots of each respective species showed few significant differences. However where these significant differences did occur, TAC levels of small roots were greater. McConnell and Garrison (1966) found that Purshia tridentata roots less than ¼ inch contained a higher percent concentration of CHO than roots greater than ¼ inch. Purshia stems over one year of age had the lowest percent concentration of CHO. Coyne and Cook (1970) investigated carbohydrate trends of five cold desert shrubs. They found that CHO concentrations were consistantly higher in root tissue than in crown tissue.

The CHO cycles of plant parts of mountain mahogany and turbinella oak generally did not show strong seasonal trends. There were numerous oscillations in CHO levels throughout the year, however, few of these oscillations represented significant changes in CHO concentrations. Generally, periods of minimum concentration were significantly lower than the periods of maximum accumulation only. Statistically, CHO trend differences may be discussed only in terms of peak periods of accumulation. Mooney and Hays (1973) also found a lack of strong seasonal trends in the tissue of the evergreen tree, coastal live oak, Quercus agriboilia. They speculated that the leaves of coastal live oak channelled CHO directly to the fruits as they developed, and to the stems during the period of new growth. In addition, Kramer and Kozlowski (1960) reported that, generally, the CHO cycles of evergreen plants showed less annual fluctuation than cycles of deciduous species.

The CHO levels of all root samples of Quercus turbinella and Cercocarpus betuloides, except large oak roots on the east exposure, had significant peaks in CHO accumulation on 1-15-77, during winter rest. This winter increase was consistant with the findings of Kramer and Kozlowski (1960) that evergreen plants tend to accumulate CHO during winter dormancy, due to cessation of tissue elongation and reduced respiration rates.

Differences in CHO accumulation apparently due to location, such as exhibited by both species in this study, were noted in research conducted by Hepting (1945) on food storage and little leaf disease in short leaf pine, Pinus echinata. Hepting sampled CHO levels in root bark, root wood, stem bark and stem wood of healthy trees in Alabama and North Carolina. He found good agreement in the CHO cycles of the trees from these two locations, except for an unexplained dip in the June root bark of the Alabama trees. The erratic fluctuation observed in CHO cycles of shrub live oak large roots on the east exposure, likewise, is not without precedent. Coyne and Cook (1970) found an erratic fluctuation in CHO trends of roots and crowns of black sage. Donart (1969) found an unexplained fluctuation in CHO concentration throughout the period of build-up in root reserves of Symphoricarpos vaccinoiodes and Chrysothamnus viscidiflorus. Menke (1973), in a two year study, found that available CHO levels in basal tissue of Atriplex confertitolia increased over winter in 1971 and decreased during bud swell. He found these trends reversed in the following year.

Seasonal trends of CHO storage in stems of Cercocarpus betuloides and Quercus turbinella were less pronounced than in roots. Generally, there were fewer periods of increased CHO storage. When these periods did occur, they were of a lesser relative magnitude than exhibited by root tissue. In fact, there were no significant differences in CHO levels of Quercus stems on the west exposure at any of the twenty sampling dates. Cercocarpus stems, on this exposure, showed

only two significant differences throughout the entire year. McConnell and Garrison (1966) had similar findings in their work with Purshia tridentata. They discovered that root material of Purshia showed greater seasonal change in CHO level than did top material.

CONCLUSIONS

The CHO cycles of Cercocupus betuloides and Quercus turbinella did not show strong seasonal CHO trends. This made it difficult to show relationships between environmental factors, phenology, and CHO trends of the two species. Regression models constructed for this purpose, had little descriptive power. However, these models did show a general association between lower air temperatures and higher CHO levels of mountain mahogany plant parts.

There were numerous oscillations in CHO levels of shrub live oak and mountain mahogany. However, the CHO trends of these plants were characterized by peak periods of accumulation rather than periods of depletion. Generally, periods of minimum concentration were significantly lower than the periods of maximum accumulation only. There were high TAC concentrations in root tissue of both species during the phenological stage winter rest, with exception of shrub live oak roots on the west exposure. Large and small mountain mahogany roots on the east exposure had a second period of accumulation at the outset of summer quiescence. There were unexplained fluctuations in TAC levels throughout the period of CHO build up in Quercus large roots on the east exposure.

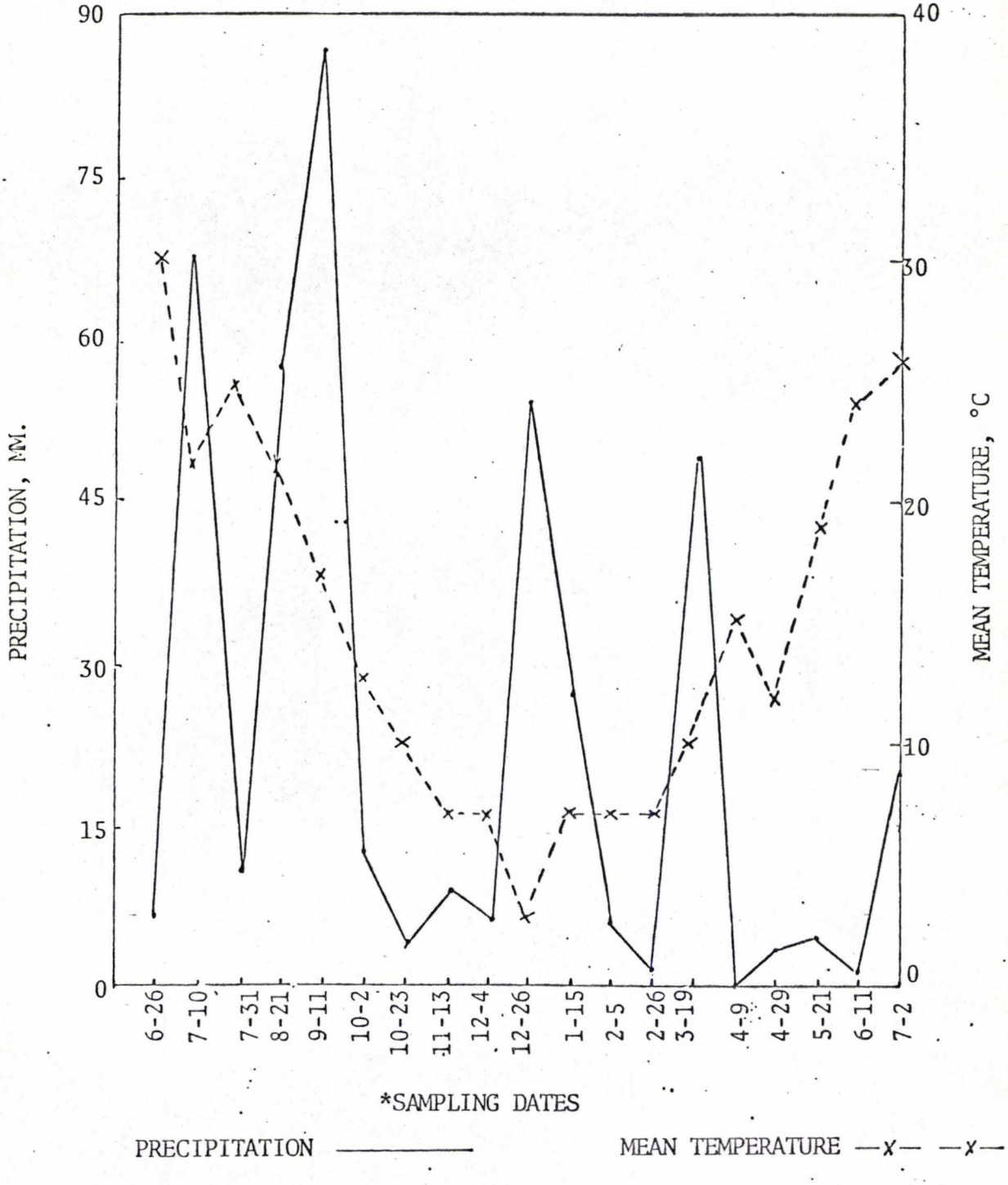
There were no dramatic low points in the CHO cycles of either plant investigated. However, both species seemed to have somewhat lower TAC concentration in the spring and fall than summer and winter.

Generally, mountain mahogany plant parts had greater CHO concentrations than shrub live oak plant parts. Root tissue of both species had a higher concentration of available carbohydrate than stem tissue.

APPENDIX A

Precipitation and Temperature

Figure 1. Precipitation and mean daily temperatures during three week sampling periods at the east exposure study area (July 1976-July 1977).



*Excluding 4-23-77

Figure 2. Maximum and minimum air temperatures at the east exposure study area (°C).

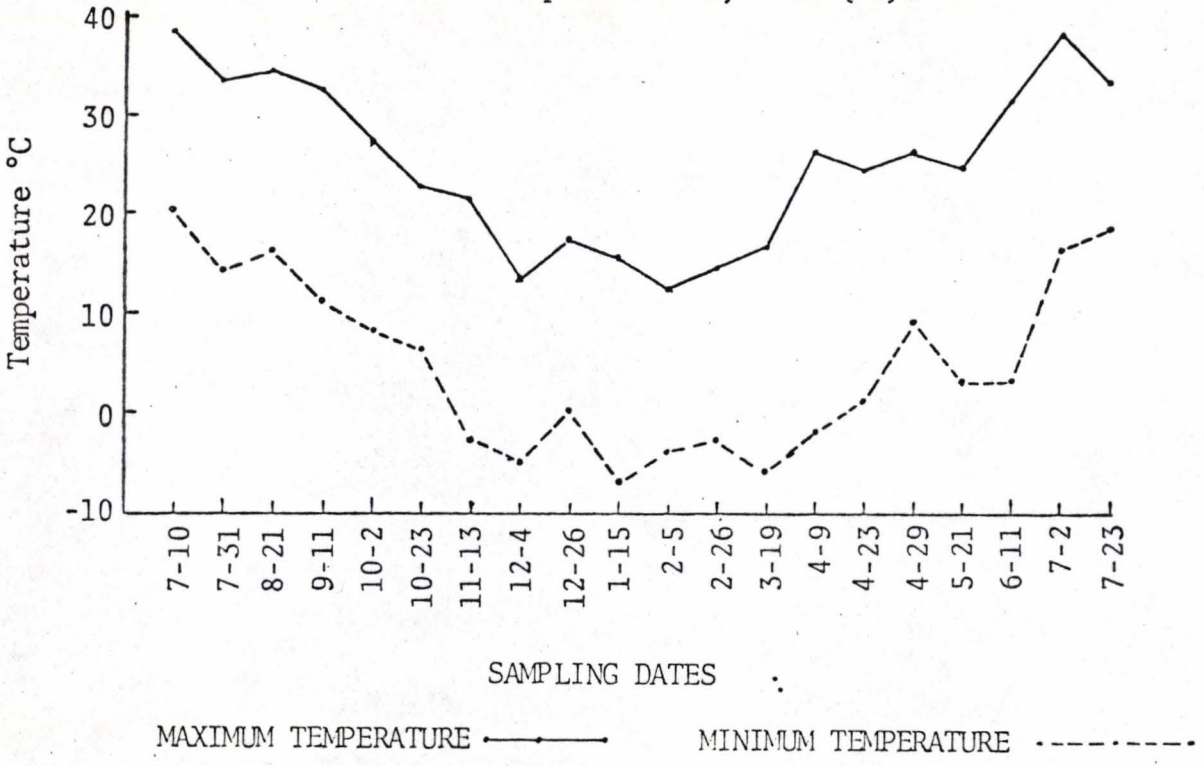
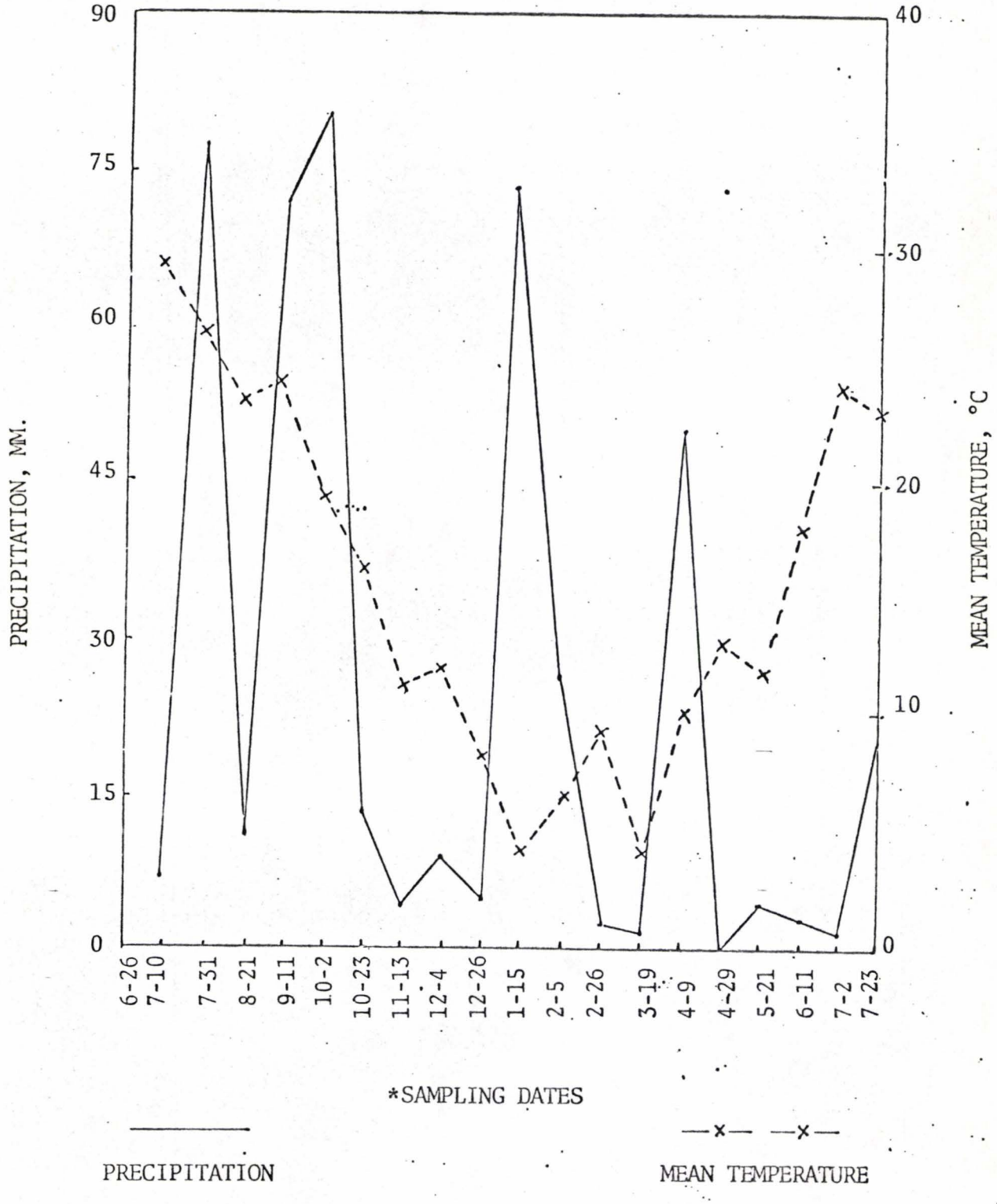


Figure 3. Precipitation and mean daily temperatures during three week sampling periods at the west exposure study area (July 1976-July 1977).



*Excluding 4-23-77

Figure 4. Maximum and minimum air temperatures at the west exposure study area (°C)

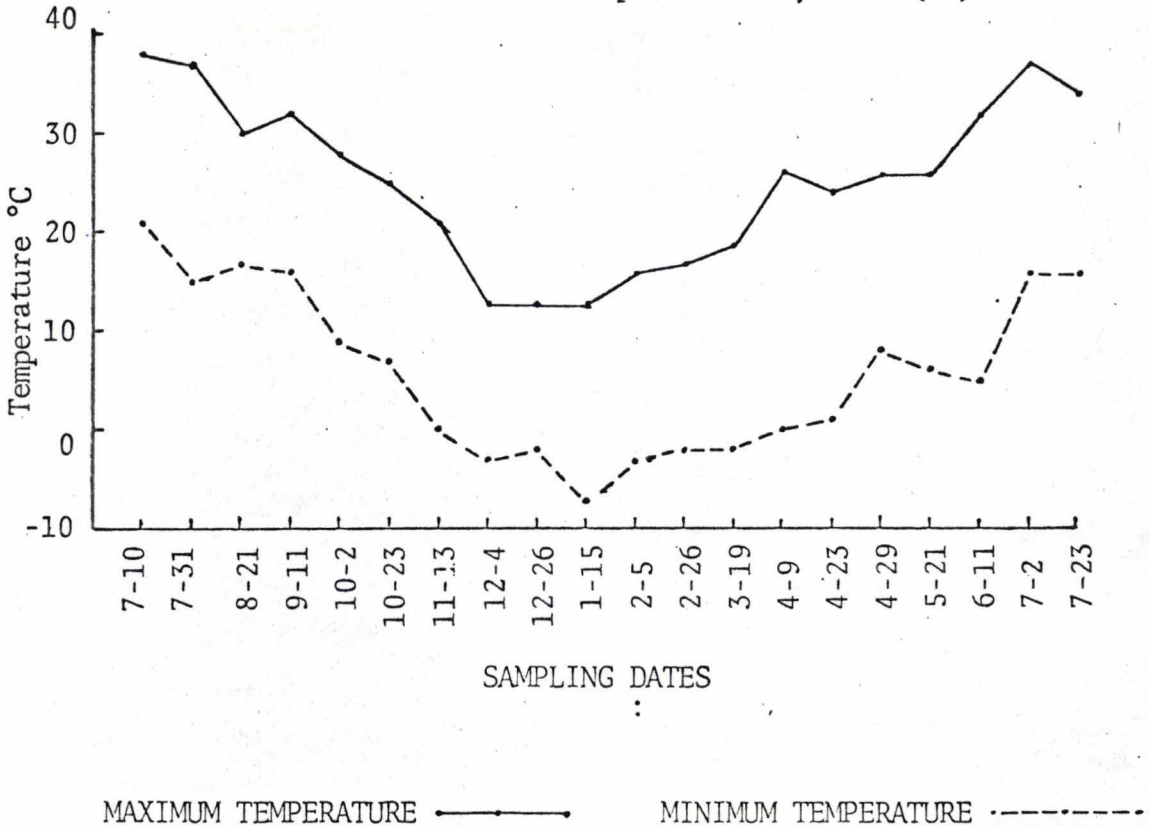


Figure 1. Soil Moisture (%) at 5 and 20 cm below the soil surface at the east exposure study area.

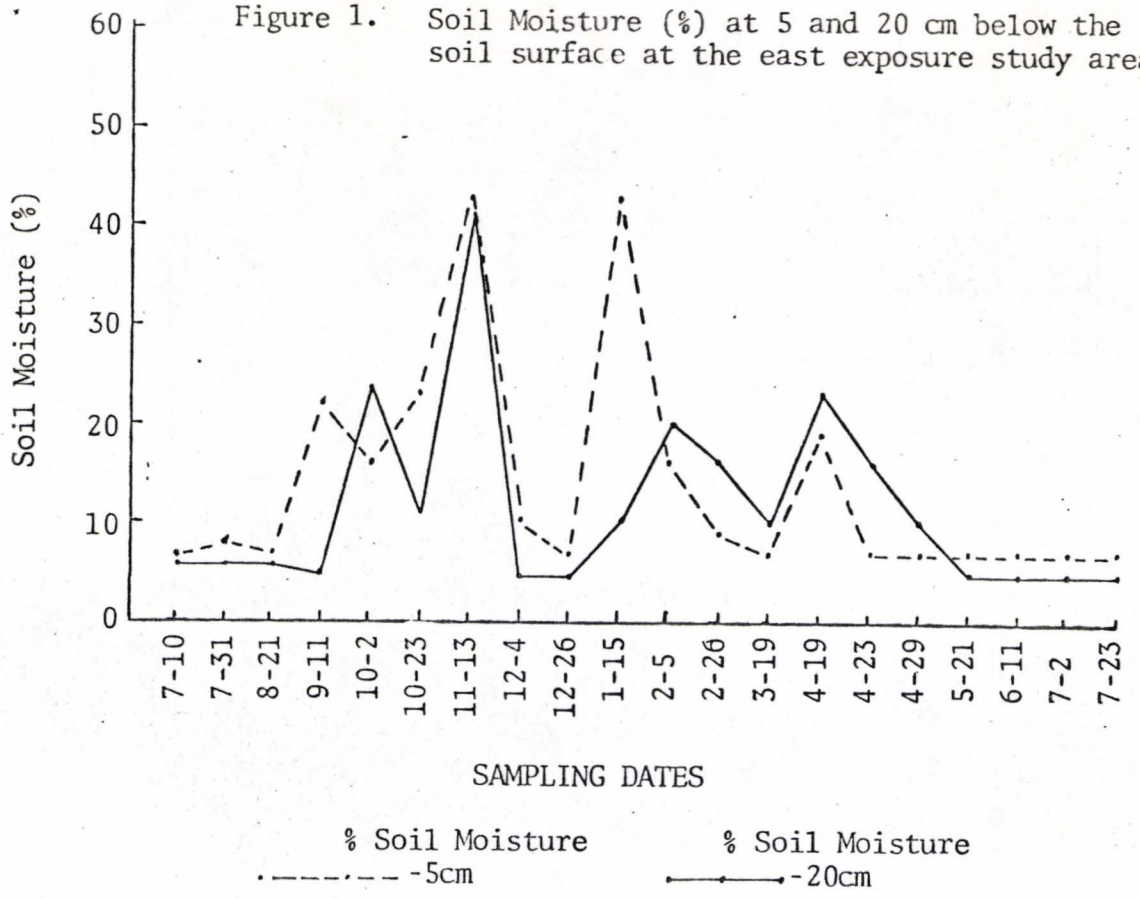


Figure 2... Soil moisture (%) at 40 and 80cm below the soil surface at the east exposure study area.

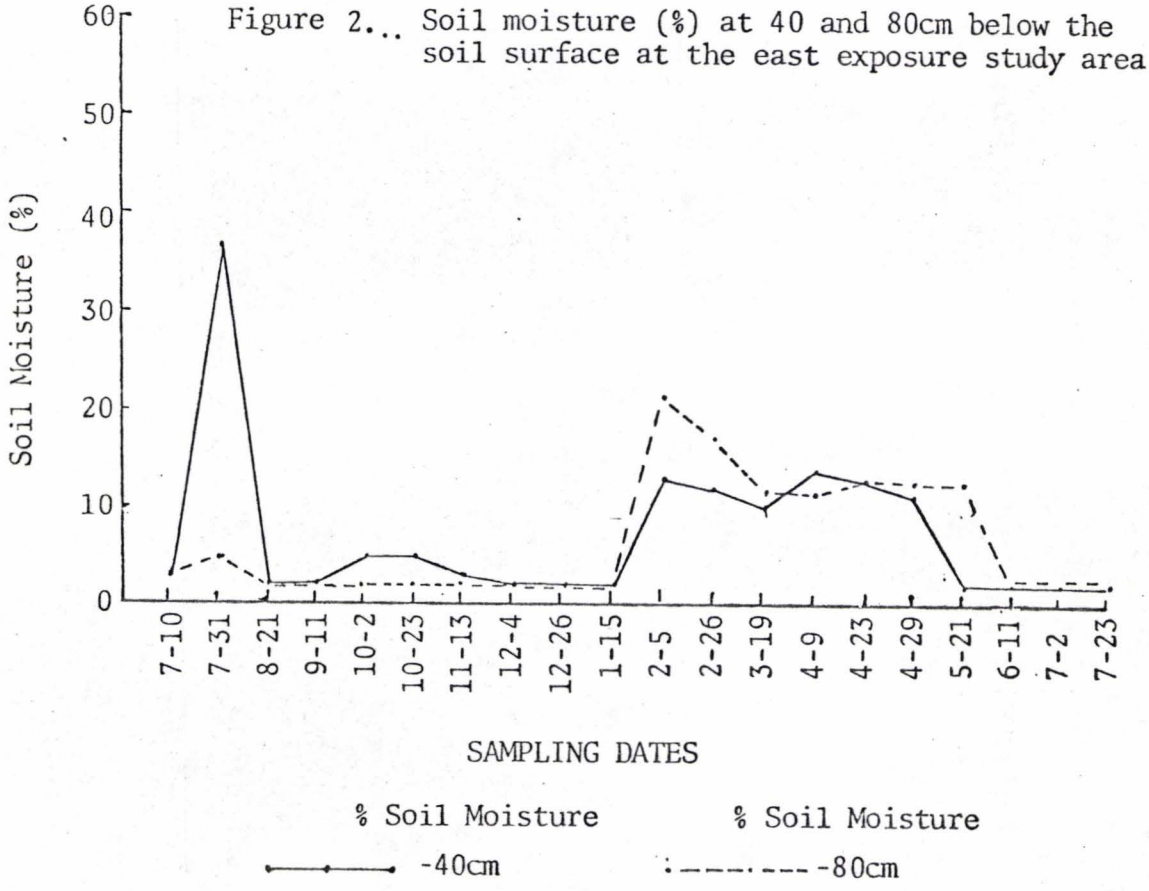


Figure 3. Soil moisture (%) at 5 and 20 cm below the soil surface at the west exposure study area.

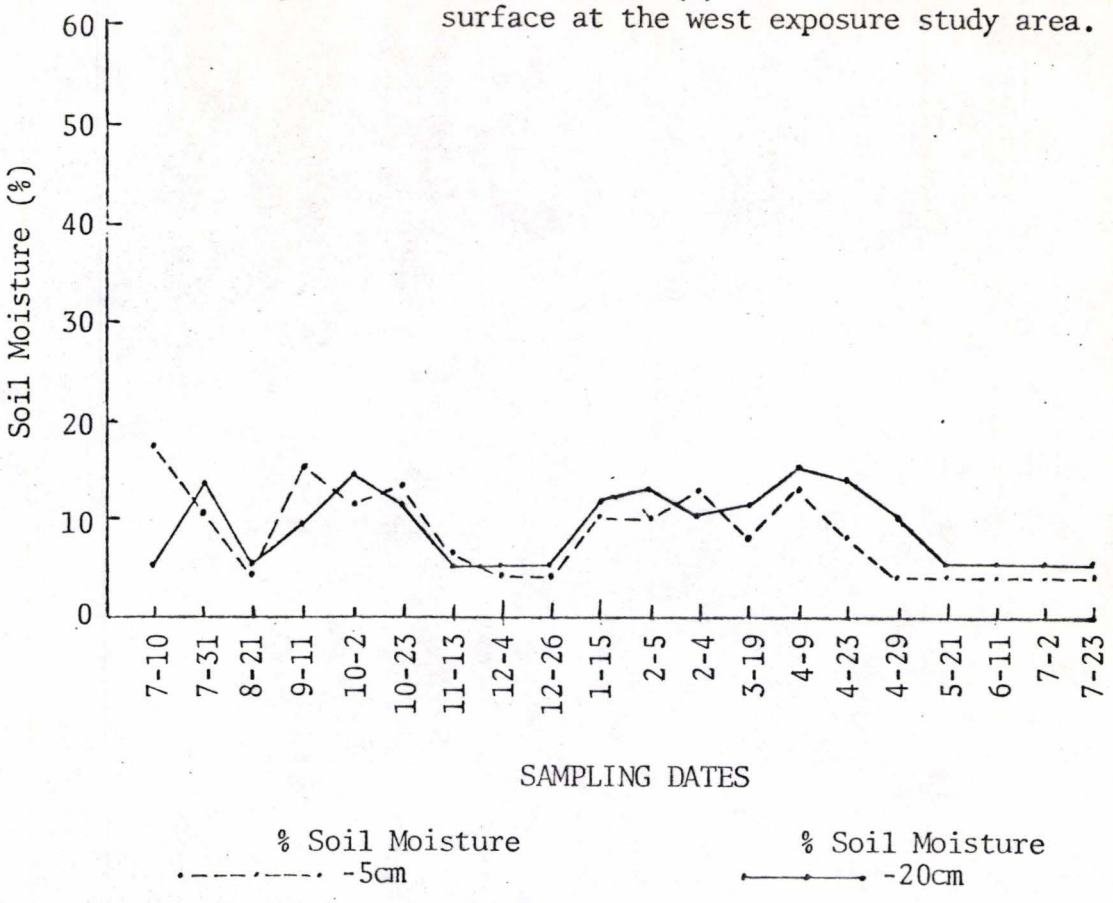
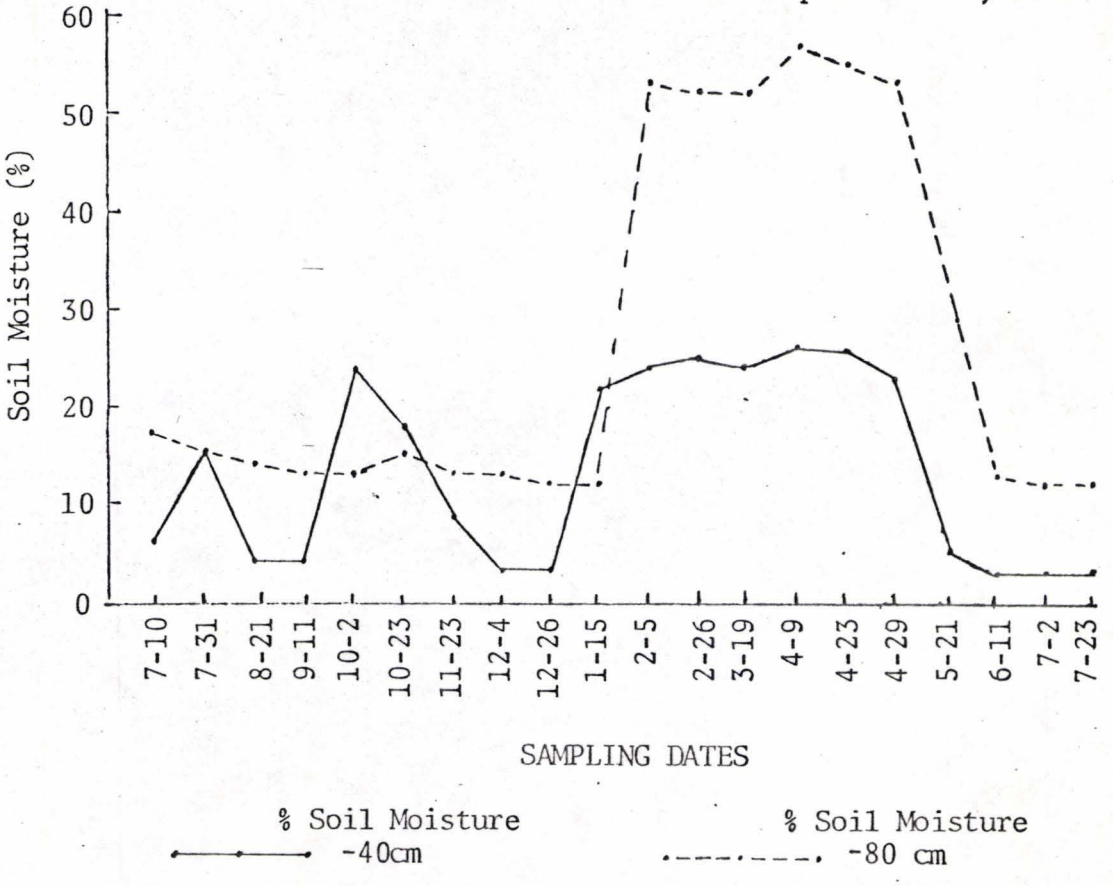


Figure 4. Soil moisture (%) at 40 and 80 cm below the soil surface at the west exposure study area.



LITERATURE CITED

Association of Official Agricultural Chemists. 1965. Official Methods of Analysis. 10th ed. Wash., D.C. 498-499.

Blaser, R.E., R.H. Brown, and H.T. Bryant. 1966. The relationship between carbohydrate accumulation and growth of grasses under different microclimates. Proc. 10th Inter. Grass Congr. 147-150.

Boo, R.M. and R.D. Pettit. 1975. Carbohydrate reserves in roots of sand shin oak in West Texas. J. of Range Management. 28(6): 469-472.

Brown, R.H. and R.E. Blaser. 1965. Relationship between reserve carbohydrate accumulation and growth rate in orchardgrass (Dactylis glomerata L.) and tall fescue (Festuca arundinacea). Crop Sci. 5: 577-582.

Brown, R.H. and R.E. Blaser. 1970. Soil moisture and temperature effects on growth and soluble carbohydrates of orchardgrass (Dactylis glomerata). Crop Sci. 10: 213-216.

Cameron, S.H., R.T. Mueller, A. Wallace, and E. Sartori. 1952. Influence of age of leaf, season of growth, and fruit production on the size and inorganic composition of Valencia orange leaves. Proc. Am. Soc. Hort. Sci. 60: 45.

Carmichael, R.S. 1976. Chaparral vegetation of the Mazatzal Mountains, Arizona. M.S. Thesis. Arizona State University, Tempe. 80 p.

Colby, W.G., M. Drake, H. Oohara, and N. Yoshida. 1966. Carbohydrate reserves in orchardgrass. Proc. 10th Inter. Grass Congr. 151-155.

Cook, C.W. 1966. Carbohydrate reserves in plants. Utah Agr. Exp. Sta. Resources Series 31. 47 p.

Cormack, D.B. and G.C. Bate. 1976. Seasonal fluctuation of total non-structural carbohydrate levels within the Macadamia integrifolia cultivar Kakea and its relation to shoot extension. Rhodesian J. Agr. Res. 14(1): 39-45.

Coyne, R.L. and C.W. Cook. 1970. Seasonal carbohydrate reserve cycles in eight desert range species. J. Range Management. 23(6): 438-444.

Dina, S.J. and L.G. Klikoff. 1973. Effect of plant moisture stress on carbohydrate and nitrogen content of big sage brush. J. Range Management. 26: 207-209.

Donart, G.B. 1969. Carbohydrate reserves of six mountain range plants as related to growth. J. Range Management. 22(6): 411-415, illus.

Eaton, F.M. and D.R. Ergle. 1948. Carbohydrate accumulation in the cotton plant at low moisture levels. Plant Physiol. 23: 169-187.

Feltner, K.C. and M.A. Massengale. 1965. Influence of temperature and harvest management on growth, level of carbohydrate in roots, and survival of alfalfa (Medicago sativa L.). Crop Sci. 5: 585-588.

Freeland, R. O. 1944. Apparent photosynthesis in some conifers during the winter. Plant Physiol. 19: 179-185.

Heinze, P.H. and A.E. Murneek. 1940. Comparative accuracy and efficiency in determination of carbohydrates in plant material. Missouri Agr. Exp. Sta. Res. Bull. 314. 23 p.

Hepting, G.H. 1945. Reserve food storage in shortleaf pine in relation to little leaf disease. Phytopathology. 35: 106-119.

Jameson, D.A. 1963 Responses of individual plants to harvesting. Bot. Rev. 29: 532-594.

Kramer, P.J. and T.T. Kozlowski. 1960. Physiology of trees. New York : McGraw-Hill. 642 p.

Laude, H.M., M.B. Jones, W.E. Moon. 1961. Annual variability in indicators of sprouting material potential in chamise. J. Range Management. 14: 323-326.

Maranville, J.W. and G.M. Paulsen. 1970. Alteration of carbohydrate composition of corn (Zea mays L.) seedlings during moisture stress. Agron. J. 62: 605-608.

McCarty, E.C. 1935. Seasonal march of carbohydrates in Elymus ambiguus and Muhlen bergia gracilis and their reaction under moderate grazing use. Plant Physiol. 10: 727-738.

McCarty, E.C. and R. Price. 1942. Growth and carbohydrate content of important mountain forage plants in central Utah as affected by clipping and grazing. U.S.D.A. Tech. Bull. 818. 51 p.

McConnell, B.R. and G.A. Garrison. 1966. Seasonal variations of available carbohydrates in bitter brush. J. Wildlife Management. 30: 168-172.

Menke, J.W. 1973. Effects of defoliation on carbohydrate reserves, vigor and herbage yield for several important Colorado range species. Univ. Microfilms Int. 283 p.

Mooney, H.A. and W.D. Billings. 1960. The annual carbohydrate cycle of alpine plants as related to growth. Amer. J. Bot. 47(7): 594-598.

Mooney, H.A. and R.I. Hays. 1973. Carbohydrate cycles in two Californian mediterranean-climate trees. Flora, German Democratic Republic. 162: 295-304.

Mooney, H.A., D.J. Parsons, and J. Kummerow. 1974. Seasonal course of plant development in mediterranean climates. In: Phenology and Seasonality Modeling. H. Leith, Ed. Springer Verlag.

Sablon, L. Du. 1906. Recherches physiologiques sur les matieres de reservers des arbres. II. Rev. Gen. Bot. 16: 341-368.

Smith, D. G.N. Paulsen, and C.A. Raguse. 1964. Extraction of total available carbohydrates from grass and legume tissue. Plant Physiol. 39: 960-962.

Smith, P.F., W. Reuther, and A.W. Specht. 1952. Seasonal changes in Valencia orange trees. II. Changes in micro-elements, sodium and carbohydrates in leaves. Proc. Am. Soc. hort. Sci. 59: 31.

Sosebee, R. E. and H.H. Wiebe. 1971. Effect of winter stress and clipping on photosynthate translocation in two grasses. Agron. J. 63: 14-17.

Sullivan, J.T. and V.G. Sprague. 1949. The effect of temperature on the growth and composition of the stubble and roots of perennial rye grass. Plant Physiol. 24: 706-719.

Trlica, M.J., Fr. 1971. Defoliation and soil moisture regime effects on plant regrowth and carbohydrate reserve utilization and storage in eight desert range species. Ph.D. Dissertation, Utah State Univ. Logan. 122 p.

Troughton, A. 1957. The underground organs of herbage grasses. Commonwealth Bur. Pastures and Field Crops Bull. 44. 163 p.

Watkins, V.M. and H. DeForest. 1941. Growth in some chaparral shrubs in California. Ecology. 22: 79-83.

Weinmann, H. 1961. Total available carbohydrates in grasses and legumes. Herbage Abstr. 31: 255-261

Wenger, K.K. 1953. The sprouting of sweetgum in relation to season of cutting and carbohydrate content. Plant Physiol. 28: 35-49.

Wilson, R.T., B.E. Dahl, D.R. Krieg. 1975. Carbohydrate reserves in mesquite roots in relation to phenological stage and reproductive condition. J. Range Management 28(4): 286-289.

Winkler, A.J. and W.O. Williams. 1945. Starch and sugars of Vitis vinifera. Plant Physiol. 20: 412-432.

Wood, F.W. H.C. Harris, R.E. Caldwell. 1959. Monthly variations of carbohydrates and nitrogen in roots of sandhill oak and wire grass. Ecology 40: 292-295.

Wright, H.A. and K.J. Stinson. 1970. Response of mesquite to season of top removal. J. Range. Management 23: 127-128.